Primates

Eye preferences in capuchin monkeys (Sapajus apella)

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ORIGINAL ARTICLE

Eye preferences in capuchin monkeys (*Sapajus apella*)

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Abstract

This study explored whether capuchin monkey eye preferences differ systematically in response to stimuli of positive and negative valence. Eleven captive capuchin monkeys were presented with four images of different emotional valence and social relevance, and eye preferences for viewing the stimuli through a monocular viewing hole were recorded. Eye preferences were found at the individual-level but not at the population-level. Furthermore, the direction of looking, number of looks and duration of looks did not differ significantly with the emotional valence of the stimuli. These results are inconsistent with the main hypotheses about the relationship between eye preferences and processing of emotional stimuli. However, the monkeys did show significantly more arousal behaviours (vocalisation, door-touching, self-scratching and hand-rubbing) when viewing the negatively valenced stimuli than the positively valenced stimuli, indicating that the stimuli were emotionally salient. These findings do not provide evidence for a relationship between eye preferences and functional hemispheric specialisations, as often proposed in humans. Additional comparative studies are required to better understand the phylogeny of lateral biases, particularly in relation to emotional valence.

Keywords Eye preferences · Behavioural laterality · Hemispheric specialisations · Emotion · Capuchin monkeys

Introduction

Behavioural laterality in primates has been widely and intensively studied for decades (Fitch and Braccini 2013; Ward and Hopkins 1993), such as hand preferences (e.g. Humle and Matsuzawa 2009), eye preferences (e.g. Westergaard and Suomi 1996b) and auditory preferences (e.g. Lemasson et al. 2010). Studies on these lateral biases are important because these are believed to be closely connected to cerebral hemispheric specialisations (Rogers et al. 2013). In primates, for example, the left hemisphere is responsible for focused attention to invariable stimuli, following learned rules and categorising stimuli, and can inhibit the right hemisphere. The right hemisphere is responsible for face perception (Tomonaga 1999; Dahl et al. 2013), spatial cognition, non-focused attention to novel stimuli, emergency responses involving intense emotions such as fear and rage, and negative cognitive bias (Rogers et al. 2013). These hemispheric specialisations are thought to be reflected in the contra-lateral of the body in preferences for movement (e.g. hand preferences) and perception (e.g. eye preferences) (Bisazza et al. 1998).

How emotional processing is specialised in each hemisphere is still controversial. There are two main hypotheses: the 'right hemisphere hypothesis' proposes that the left hemisphere is dominant for cognitive processing and the right hemisphere is dominant for emotional processing (Borod et al. 1998), whilst the 'valence hypothesis' proposes that the right hemisphere is dominant for negative emotional processing and the left hemisphere is dominant for positive emotional processing (Davidson 1995). In addition, the 'motivational approach-withdrawal hypothesis' compliments the valence hypothesis and proposes the left hemisphere drives approach behaviour towards stimuli, and the right hemisphere drives withdrawal behaviour away from stimuli (Demaree et al. 2005).

In human and non-human primates, empirical evidence suggests the right hemisphere is dominant for emotional processing (Lindell 2013). For example, in humans, Adolphs et al. (1996) found damage to the right hemisphere impairs the ability to identify and discriminate facial emotions, whereas damage to the left hemisphere does not. In non-human primates, Vermeire and Hamilton (1998) found split brain rhesus macaques were significantly better at discriminating emotional facial expressions when presented through a single eyehole to the isolated right hemisphere than to the isolated left hemisphere.

However, few studies have investigated the relationship between emotional processing and visual laterality in non-human primates. Visual laterality is typically investigated in non-human primates using eye preference (e.g. Kounin, 1938), visual field (e.g. Vauclair et al. 1993) and head orientation (e.g. Casperd and Dunbar, 1996) measures. The results of such studies do not provide consistent support for either the right hemisphere or valence hypotheses (Chapelain and Blois-Heulin 2009).

In eye preference studies using stimuli of both positive and negative valence, Hook-Costigan and Rogers (1998) found support for the valence hypothesis in common marmosets; a right eye preference (left hemisphere dominance) for viewing food (banana) and a shift to left eye preference (right hemisphere dominance) for viewing a model snake (although see Rogers et al. 1994, for opposite findings in small-eared bush babies). More recently, Braccini et al. (2012) found support for the valence hypothesis when they examined eye preferences in captive adult chimpanzees for various stimuli; the strongest right eye preference for food (banana) and the strongest left eye preference for a plastic snake was found. In addition, the chimpanzees looked more frequently and

for longer at the positive stimuli, and less frequently and for shorter at the negative stimuli, consistent with the motivational approach-withdrawal hypothesis.

The aim of the present study was two-fold. Firstly, to examine eye preferences in capuchin monkeys, a species popular for behavioural and cognitive research. There are some reports on eye preferences in capuchin monkeys for viewing food rewards (Kounin, 1938) but the small sample size of three monkeys makes it difficult to determine population-level, or species-level, eye preferences in this species. In a larger scale study, Westergaard and Suomi (1996b) tested 40 capuchin monkeys and found individual-level but not group-level eye biases. However, only a single stimulus (a grape) was presented at the end of a tube. Therefore, secondly, we aimed to examine whether eye preferences were modulated by the emotional valence of the stimuli presented, including social stimuli not previously tested in this paradigm. In particular, we tried to test whether capuchin monkeys also show a pattern of eye preference consistent with the valence and motivational approach-withdrawal hypotheses. On this basis, we predicted they would prefer to view positively valenced stimuli with their right eye (more frequently and for a longer duration) and negatively valenced stimuli with their left eye (less frequently and for a shorter duration).

Methods

Participants and housing

Eleven tufted capuchin monkeys (*Sapajus apella*) were studied at the Living Links to Human Evolution Research Centre located at the Royal Zoological Society of Scotland's Edinburgh Zoo (UK). Nine males and two females took part in the experiment (age range two to thirteen years old) and all but one monkey was captive

born. The capuchin monkey's indoor enclosure measured 32.5 m². The monkeys were habituated to the research cubicle environment and could voluntarily enter a test cubicle for short periods of isolation. The study was approved by the Research Ethics Review Committee at the University of Edinburgh, UK, and complied with regulations of the Association for the Study of Animal Behaviour (ASAB 2012).

Apparatus

The experiment was conducted in research rooms, in which a set of eight research cubicles ($0.5m^3$ each) were arranged. The monkeys voluntarily accessed the research cubicles through an entrance from their outdoor enclosure. Transparent or opaque slide doors allowed individual cubicles to be opened to or closed off from each other. Each cubicle had windows to allow the monkeys to be easily observed.

The viewing apparatus was a cardboard panel (37.0 cm x 33.8 cm) which slotted into the front of the research cubicle door with an eight mm in diameter viewing hole (11 cm from the top of the panel). A 17'' LCD monitor (Dell, E177FPc, Round Rock, Texas) was used to present stimuli using Microsoft PowerPoint. The monitor was placed on a 120 cm high stand at a distance of 50 cm from the research cubicle door.

To record eye preferences a video camera was placed directly on top of the research cubicle and angled downward to capture the position of the top of the monkey's head in relation to the viewing hole. A second video camera was set at the far end of the research cubicles to record general behaviour and hand preferences when reaching for food rewards (Fig .1).

Stimuli

Four stimuli (trimmed photographs against a black background) were presented per test session consisting of two positively and two negatively valenced stimuli, which were either social (featured capuchin monkey facial expressions) or non-social (did not feature capuchin monkeys). The non-social positively-valenced stimulus was a boiled egg, a favourite food in their daily diet. The non-social negatively-valenced stimulus was an open-mouth harpy eagle face, a natural predator (Fragaszy et al. 2004). The monkeys had been habituated to model snakes in previous studies, and so the harpy eagle was chosen as an alternative potentially emotive stimulus. The social positively-valenced stimulus was a capuchin monkey raised eyebrow face, which is commonly displayed by all sex and age classes during social affiliative interactions and play (Fragaszy et al. 2004). The social negatively-valenced stimulus was a capuchin monkey open-mouth threat face. The stimuli were presented successively and presentation order was counterbalanced across monkeys.

Procedure

At the start of each session monkeys entered the research cubicles from outside. After the cubicle slide door was closed, and the monkeys became briefly accustomed to the inside of the cubicle, the stimuli were presented on a screen, positioned in front of the door covered by the viewing hole panel. The monkeys were given three different cues to signal the initial presentation and subsequent change of stimuli; a computer generated camera shutter sound, calling the monkey's name by the experimenter, and tapping gently five times at the viewing hole. The experimenter handling the monkeys was blind to stimuli presentation order to avoid inadvertent cueing.

Each monkey was given up to 60 seconds to take an initial look at each stimulus. The experimenter would repeat the monkey's name and tap at the hole at 15 second

intervals until they took an initial look, or one minute elapsed. After an initial look, the image was retained for an additional 30 seconds (without providing any cues). At the end of the trial, or if an initial look was not taken within 60 seconds, the next stimulus was presented. Therefore, the shortest length of time a monkey could be in the research cubicles on any one occasion was two minutes, and the longest time six minutes. If at any point the monkeys showed specific behaviours, such as pacing rapidly, vocalising excessively, or pushing the entrance slide door, the testing session was ended. After testing, the monkeys were given food rewards and released. Participants were never rewarded for looking into the viewing hole, as this may have reinforced the use of a particular eye (Chapelain and Blois-Heulin 2009).

A look was defined as the monkey's head moving within at least two centimetres of the viewing hole and ended when the head moved two centimetres or more away. Eye use judgements were made by observing the position of the top of the monkey's head in relation to cross hairs transecting the viewing hole. Ambiguous looking behaviour, such as rapid eye switches, were excluded from the subsequent data analyses.

From initial video observations four potential arousal behaviours were identified and recorded; a 'hiccup' vocalisation (e.g. Wheeler 2010), door-touching (often preceding pushing of the cubicle slide door), self-scratching (e.g. Dufour et al. 2011; Yamanashi and Matsuzawa 2010), and hand-rubbing (often preceded by sudden withdrawal from the viewing hole and accompanied by vocalisation). Arousal behaviours were recorded within the stimulus presentation period of each session.

In addition, hand preferences were preliminarily measured by recording which hand the monkeys used when reaching for food rewards given before the start of the experiment. Three or more hand reaches were used to determine hand preference.

Inter-rater reliability

Inter-rater reliability scores were obtained by asking a second rater to code the video recordings of three monkeys. Frequency and order of observed looks, and order of arousal behaviours were recorded. Kappa coefficients were calculated for the frequency of these measures (Bakeman and Gottman 1997). Inter-rater reliability for eye use scores was .77 ($p < .001$) indicating 'substantial agreement' between raters (Landis and Koch 1977). For arousal behaviours there was 'fair agreement' on the frequency of behaviours in a particular category (Kappa = .40, $p < .001$) and 'perfect agreement' on the category to which the behaviour belonged to (Kappa = 1.0, $p < .001$).

Statistical analysis

The data were analysed using SPSS (Version 19) and R (Version 3.2.2). For each monkey, eye preferences were calculated using an eye use index measure. This was done by subtracting the total number of right eye uses (R) from the total number of left eye uses (L) and dividing by the total number = (R – L) / (R + L). Eye use index values ranged from 1.0 (complete preference for right eye use), through zero for no preference, to -1.0 (complete preference for left eye use) (Westergaard and Suomi 1996a). We also used binomial tests to evaluate the strength of eye preferences for each individual. Hand preference was calculated using the same method to generate a hand use index measure.

The mean scores for the duration of initial, and subsequent looks, and collated arousal behaviours (vocalisation, door touching, self-scratching and hand-rubbing) were

not normally distributed. Square root transformations were performed resulting in normally distributed scores (Shapiro-Wilk tests) for initial looks ($S\text{-}W_{(28)} = .97$, $p = .65$), subsequent looks ($S\text{-}W_{(28)} = .98$, $p = .94$) and arousal behaviours ($S\text{-}W_{(44)} = .97$, $p = .23$). The square roots of the mean scores for all looking and behaviour dependent variables were then analysed using a 2 x 2 repeated-measures analysis of variance (ANOVA), with emotional valence and social relevance as independent variables.

Results

Eye use

The total number of looks at an individual stimulus ranged from 1 to 16 looks. Figure 2 shows the median of the total number of looks (combined across right and left eyes) for each positively and negatively valenced category. Monkeys did not show any difference in total looks between valence categories (Wilcoxon signed-rank test, $V = 8$, $N = 11$, $p = .20$) and between social and nonsocial stimuli ($V = 14.5$, $N = 11$, $p = 1$).

Figure 3 shows the eye use index scores for each monkey. All monkeys significantly preferred using either their left or right eye (binomial tests, all $ps < .05$). However, there was no significant population-level eye preference; seven monkeys had an overall left eye preference and four monkeys had an overall right eye preference, irrespective of stimulus valence (binomial test, $p = .27$). The mean eye use index scores for valence categories based on total number of looks did not differ significantly from zero; for positively valenced stimuli the score was -0.18 ($t_{(10)} = .65$, $p = .53$) and for negatively valenced stimuli -0.30 ($t_{(10)} = 1.08$, $p = .31$). There was also no significant difference between valence categories ($t_{(10)} = 1.27$, $p = .23$). This tendency was consistent when analysed on the basis of initial looks and subsequent looks.

Four monkeys did not take subsequent looks at all four stimuli, and so were excluded from the initial and subsequent look duration analyses. For initial looks the duration ranged from 0.1 to 5.4 seconds. Mean duration was 1.38 s (egg), 1.33 s (eagle face), 1.37 s (monkey raised eyebrow face) and 1.86 s (monkey threat face). A 2 x 2 repeated measures ANOVA on the duration of initial look means found no significant main effects of valence and social stimuli type (valence; $F_{(1, 6)} = .85$, $MSE = .05$, $p = .39$, social type; $F_{(1, 6)} = 2.28$, $MSE = .04$, $p = .18$) and no interaction ($F_{(1, 6)} = 1.09$, $MSE = .09$, $p = .34$). For subsequent looks the duration ranged from 0.2 to 3.6 seconds. Mean duration was 0.58 s (egg), 0.55 s (eagle face), 0.44 s (monkey raised eyebrow face) and 0.75 s (monkey threat face). Subsequent looks were significantly shorter than first looks ($t_{(6)} = 5.84$, $p = .001$). A 2 x 2 repeated measures ANOVA on the duration of subsequent looks means found no significant main effects of valence and social stimuli type (valence; $F_{(1, 6)} = 1.10$, $MSE = .07$, $p = .33$, social type; $F_{(1, 6)} = 0.05$, $MSE = 0.10$, $p = .94$) and no interaction ($F_{(1, 6)} = 3.42$, $MSE = .03$, $p = .11$).

Arousal behaviours

Figure 4 shows the mean number of observed arousal behaviours per session as a function of stimulus condition. Given the low frequency of arousal behaviours in some sessions, all arousal behaviours were combined across sessions, and an overall mean score calculated for each individual. The analysis found a significant main effect of valence, $F_{(1, 10)} = 5.74$, $MSE = .04$, $p = .04$, which reflects more total arousal behaviours in response to viewing the negatively valenced stimuli (M = .66 observations per session) than positively valenced stimuli (M = .40 observations per session).

Relationship between eye and hand preference

Figure 3 also shows hand use index scores for each monkey. Three monkeys did not make three or more hand reaches for food and so were excluded from the analyses. Left hand preferences were shown by three monkeys and right hand preferences were shown by five monkeys. However, as clearly shown in this figure, there was no significant correlation between eye and hand use index scores ($r_{(6)} = -.17$, $p = .69$).

Discussion

This study found that eye preferences in capuchin monkeys were strongly lateralised at the individual-level; all of the monkeys looked at all the stimuli consistently with either their left or right eye. There are only two previous studies which have investigated capuchin monkey eye preferences (Kounin 1938; Westergaard and Suomi 1996b). Our results are consistent with Westergaard and Suomi (1996b), who also showed individual-level, but not group-level eye preferences using a similar monocular viewing task; 14 monkeys (41%) showed a left eye bias, 13 monkeys (38%) showed a right eye bias, and seven monkeys (21%) showed no eye bias. In comparison, our study found seven monkeys (64%) had a left eye bias and four monkeys (36%) had a right eye bias.

In both studies there was also no relationship between hand and eye preference. This is consistent with studies in both non-human primates (Braccini et al. 2012; Fitch and Braccini 2013) and humans (e.g. Mapp et al. 2003; Papousek and Schulter 1999; Pointer 2001).

There was no difference in the direction of eye preference according to the emotional valence or social relevance of the stimuli. Eye preferences did not change between the first look and subsequent looks (when the monkeys had knowledge of the stimuli). Therefore, our results do not provide support for either the valence hypothesis or the right-hemisphere hypothesis of emotional processing.

More frequent looking and for a longer duration at the positively valenced stimuli (approach behaviour) and less frequent looking and for a shorter duration at the negatively valenced stimuli (withdrawal behaviour) was predicted (Braccini et al. 2012). Although subsequent looks were significantly shorter than first looks, possibly due to habituation, there was no difference in looking frequency or duration in regards to the stimuli valence. Overall, these results do not provide any support for the motivational approach-withdrawal hypothesis.

Previous eye preference studies providing support for the valence hypothesis in non-human primates have used real objects as stimuli (e.g. Braccini et al. 2012; Hook-Costigan and Rogers 1998). In the present study we presented stimuli as two-dimensional images on a monitor screen, to allow for greater control of social stimuli presentation, and to maintain consistency across all stimuli. One possibility is that two-dimensional representation has a weaker emotional salience than three-dimensional (real) representation (cf. Fagot et al. 2000). However, our monkeys showed more arousal behaviours in response to viewing the negatively valenced stimuli than the positively valenced stimuli, suggesting the images did have a degree of emotional salience. Despite this, emotional valence did not impact upon eye preference and instead the monkeys demonstrated consistent individual eye preferences across stimuli.

Another explanation is that there is no systematic causal relationship between eye preference and hemispheric specialisations in primates. Primates have a crossing optic chiasm, which means visual information from each eye is sent to both cerebral hemispheres (Jeffrey 2001). The different thickness of the optic fibres means those crossing to the contralateral hemisphere are more dominant and transfer information faster than uncrossed fibres connected to the ipsilateral hemisphere (Bisazza et al. 1998).

298 Therefore, if mammals with greater crossing of optic fibres than primates (50%
299 decussation) such as horses (80-90% decussation) are tested (Brooks et al. 1999),
300 hemispheric specialisation for emotional processing may affect eye preference more
301 directly.

302 However, after reviewing the previous literature in humans, Mapp et al. (2003)
303 concluded that eye preference is determined by the constraint of the monocular viewing
304 task itself, and "the habit or ease of using the chosen eye", independently of
305 hemispheric specialisations. The strong individual left or right eye lateralisation found
306 in this study may simply be a reflection of this constraint, and so eye preferences may
307 not be a good measure for testing the emotional valence hypothesis. A better approach
308 to examine hemispheric specialisations for emotional stimuli, may be to present stimuli
309 to either the left or right visual field for a brief duration, such as less than 200
310 milliseconds, during which the participant cannot make goal-directed saccades (e.g.
311 Fagot and Deruelle 1997; Vauclair et al. 1993).

312 In conclusion, the findings of this study do not provide convincing support for
313 eye preferences as a measure of emotional responses in captive capuchin monkeys. The
314 current data on emotional processing and eye preferences in non-human primates
315 remains inconsistent. Thus research with a greater number of species and larger sample
316 sizes is needed to better understand the potential of eye preferences as a measure of
317 emotional processing in non-human primates.

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Compliance with Ethical Standards Conflict of Interest: The authors declare that they have no conflict of interest. Ethical Approval: The study was approved by the Research Ethics Review Committee at the University of Edinburgh, UK, and complied with regulations of the Association for the Study of Animal Behaviour (ASAB 2012).

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Figure captions

Fig. 1 A capuchin monkey ‘Kato’, adopting a bipedal standing position to look into the viewing hole from inside the test cubicle

Fig. 2 Boxplot of the total number of looks (combined across right and left eyes) for each category of stimuli presented

Fig. 3 Eye and hand use index scores for each monkey. Bars indicate eye use index and circles indicate hand use index. Minus values indicate left eye or hand preference, and plus values indicate right eye or hand preference

Fig. 4 Mean number of arousal behaviours per session. Error bars represent the standard error of the mean

Figure 1

Figure 2

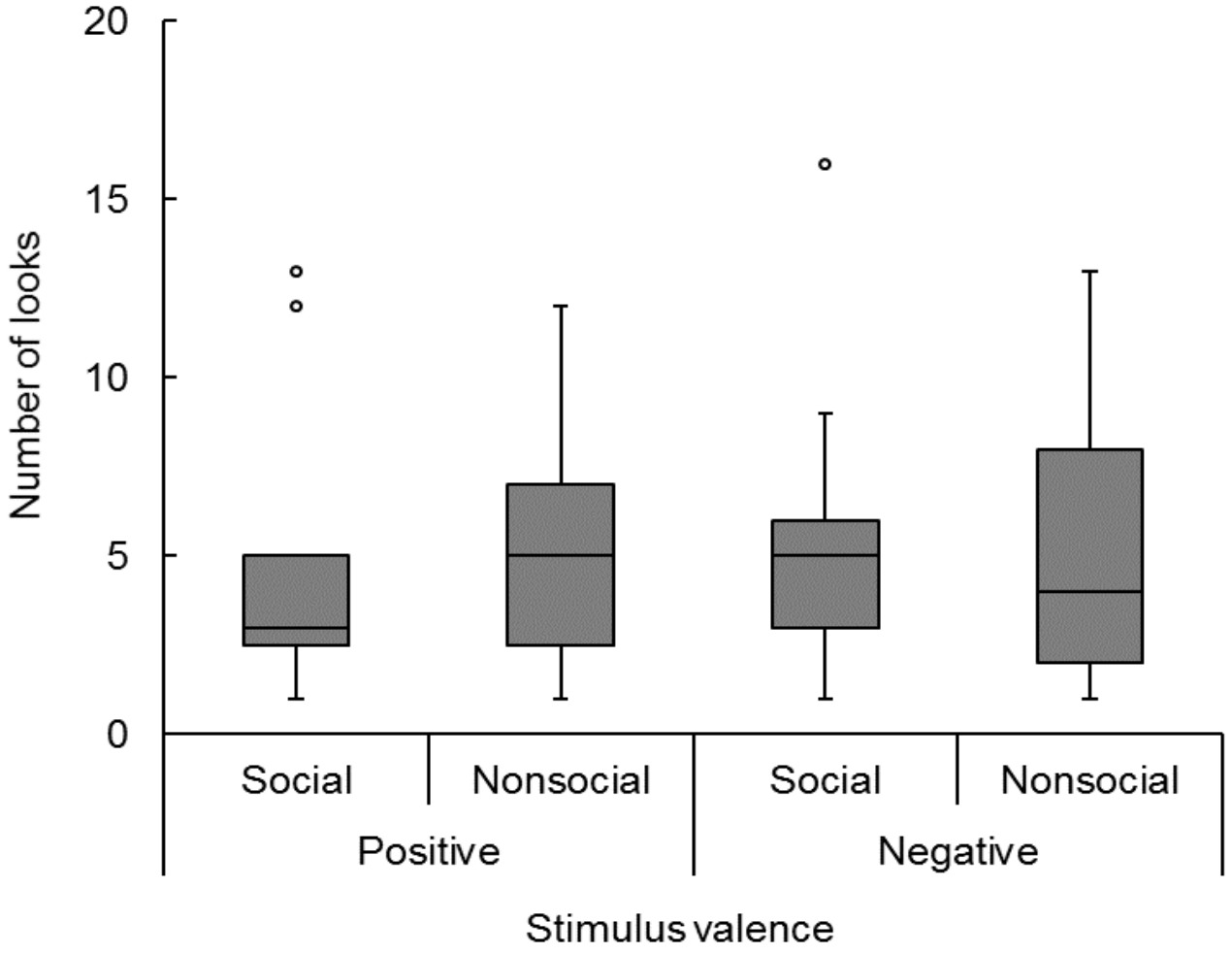

20
15
10
5
0
Number of looks
Social
Nonsocial
Social
Nonsocial
Positive
Negative
Stimulus valence

Figure 3

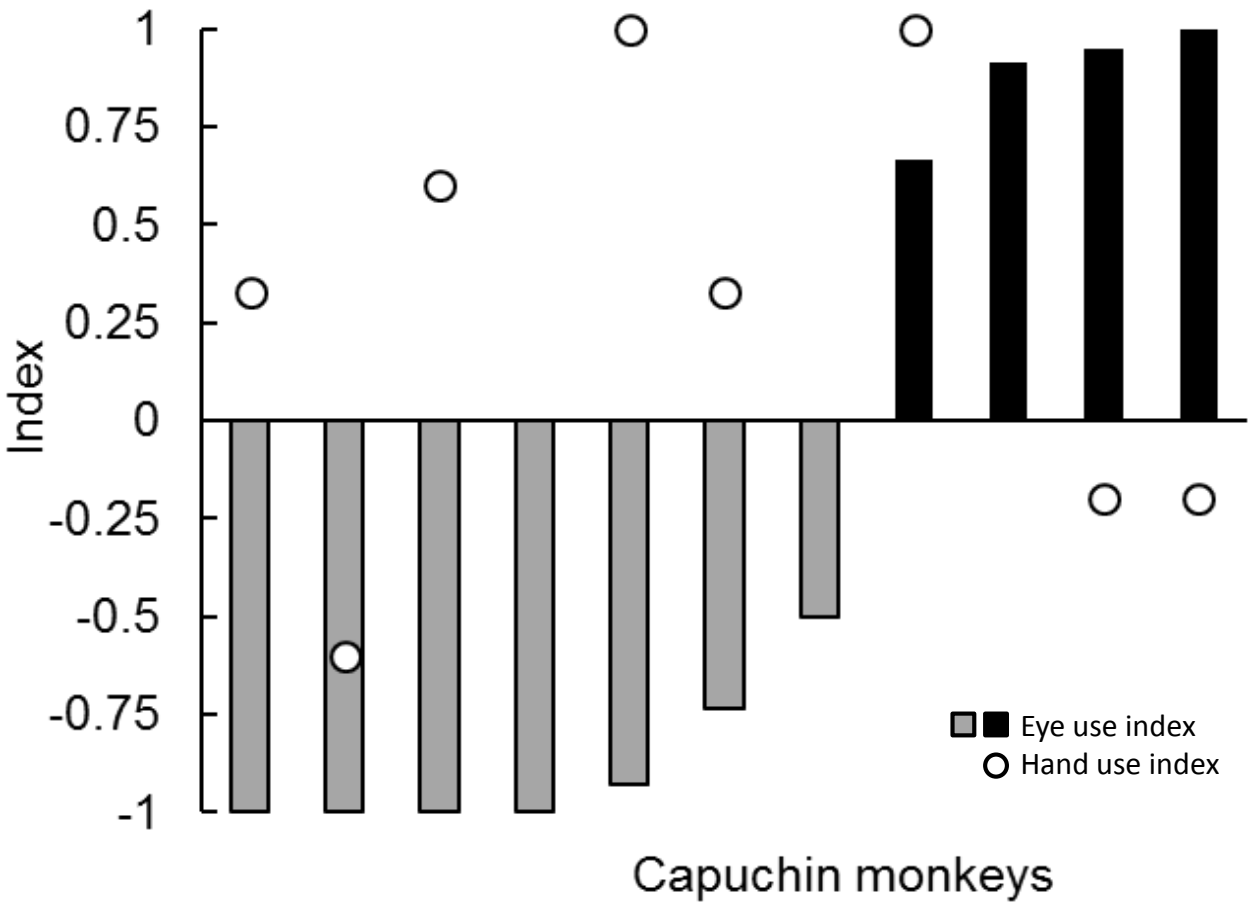
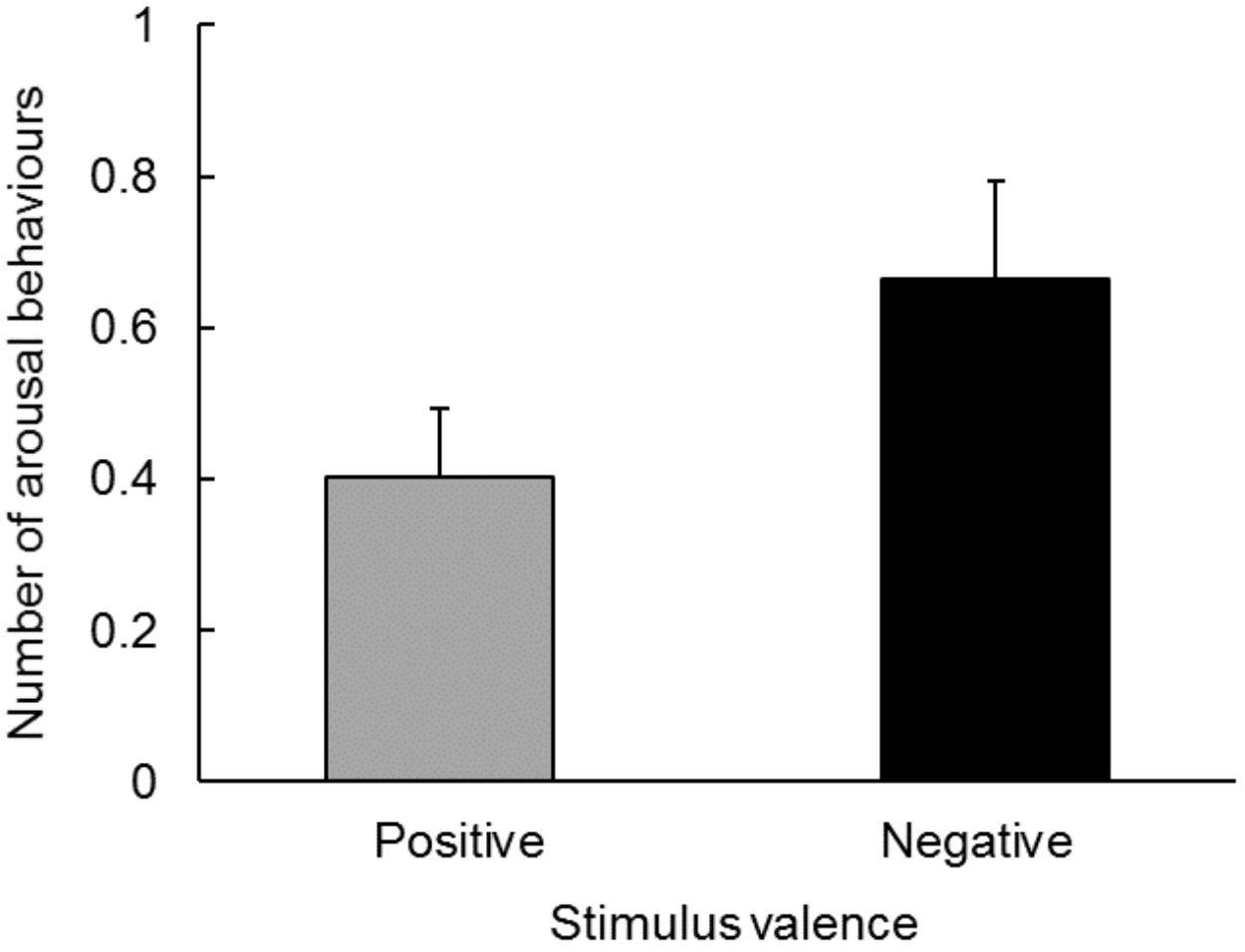

1
0.75
0.5
0.25
0
-0.25
-0.5
-0.75
-1
Index
Eye use index
Hand use index
Capuchin monkeys

Figure 4


Number of arousal behaviours
1
0.8
0.6
0.4
0.2
0
Positive
Negative
Stimulus valence